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Research article

How to study subterranean army ants: a novel method for locating and monitoring field populations of the South East Asian army ant *Dorylus (Dichthadia) laevigatus* Smith, 1857 (Formicidae, Dorylinae) with observations on their ecology

A. Weissflog[1], E. Sternheim[1], W. H. O. Dorow[2], S. Berghoff[1] and U. Maschwitz[1]

[1] *Zoologisches Institut, J. W. Goethe-Universität, Siesmayerstrasse 70, D-60054 Frankfurt am Main, Germany, e-mail: Weissflog@zoology.uni-frankfurt.de*
[2] *Forschungsinstitut Senckenberg, Senckenberganlage 25, D-60325 Frankfurt am Main, Germany*

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Summary. A new method employing palm oil as bait was developed for studying the distribution and ecology of subterranean army ants. In SE Asia the hypogaeic army ant *Dorylus laevigatus* was found to be very common in both forested and open environments. More than 10000 workers were found at individual baits. The workers cooperatively dig a three-dimensional tunnel network into the soil. Over a period of 72 days no emigrations of *D. laevigatus* could be detected, a first indication of a facultatively stationary way of life in this ant. Encounters with *Pheidologeton silenus* about food resources were observed. In feeding experiments *D. laevigatus* readily took a variety of arthropods and annelids but ignored starch containing vegetables as food. The rare hypogaeic *D. (Alaopone)* cf. *vishnui* could be collected for the first time in India and Sri Lanka. Also the epigaeic *D. (Anomma) nigricans* from Africa were found to be attracted to palm oil. The oil-method thus provides the opportunity to detect and monitor populations of army ants of the genus *Dorylus* in tropical and subtropical habitats.

Key words: Army ants, hypogaeic, Dorylinae, novel method.

Introduction

A spectacular and characteristic life form of tropical and subtropical habitats is represented by army ants. Their highly co-ordinated mass raids, sometimes comprising millions of co-operating workers, have been noted by fascinated naturalists more than a century ago (Bates, 1884; Belt, 1874; Lund, 1831).

Their frequent colony emigrations, their way of nesting and their cyclic brood rearing are impressively well organized. These are reasons why army ants have attracted much attention and are among the best studied of all social animals (Gotwald, 1995). The two Old World ant subfamilies Dorylinae and Aenictinae and the New World Ecitoninae are regarded as the typical army ants (Hölldobler and Wilson, 1990). Army ant behavior was also discovered and described in Asia in the ponerine genus *Leptogenys* (Maschwitz et al., 1989). Though extensively studied and very well known through a steadily growing number of papers and books (e.g., Schneirla, 1971; Hölldobler and Wilson, 1990; Gotwald, 1995), a thorough look at our knowledge on army ants, presents a paradox. Virtually all studies on army ant sociobiology deal with epigaeic species. The vast majority of army ant species, however, are completely subterranean (Rettenmeyer et al., 1983; Gotwald, 1995). For example, about 75% of all species of the genus *Dorylus* so far described are hypogaeic. The comparatively few epigaeic species have evolved from hypogaeic ancestors (Gotwald, 1985, 1988). Thus our knowledge on the sociobiology of these ants is based on studies of some advanced specialists. Whether the general behavioral features like group raiding, nomadism, bivouac nesting, cyclic brood development, etc., which characterize army ant sociobiology (Wilson, 1958), are typical for all these ants or only special characteristics of a few advanced species remains unknown.

The reason for this complete lack of knowledge on all aspects of sociobiology and even on faunistic distribution of hypogaeic army ants is the fact that until now no methodological approach existed to investigate them. Knowledge on the Indo-Australian Dorylinae is especially poor. Because of a special biogeographic situation no epigaeic Dorylinae exists (Gotwald, 1977). Only four exclusively hypogaeic *Dorylus* species belonging to three different subgenera are known from Sri Lanka and India to the continental and Western Malesian region (Wilson, 1964). Particularly in Peninsular Malaysia, Sumatra and Borneo, *Dorylus* species are thought to be very rare. This is supported by the fact that besides five reports (Bolton, 1995) restricted to taxonomy, no records on *Dorylus* in this region exist. During our long term studies on *Leptogenys* and *Aenictus* in Peninsular Malaysia, we found the army ant *Dorylus laevigatus* only a few times by chance. Then one of us (AW) discovered that these ants could be easily attracted by palm oil applied to and soaking the soil. The same applies to other *Dorylus* spp. This method allows a specific survey of geographical distribution of *Dorylus* army ants as well as the investigation of many questions of their sociobiology. We expect that our novel method will help expand the knowledge on hypogaeic army ants in SE-Asia and elsewhere substantially.

Here we report (1) on this simple, inexpensive method for accessing and monitoring hypogaeic species of the genus *Dorylus*, (2) about the geographic and habitat distribution of *D. laevigatus* colonies, (3) about the feeding preferences and some behavioral patterns of *D. laevigatus*, and, finally (4) the attraction to oil by other *Dorylus* spp. in Asia and Africa.

Material and methods

Species of the genus *Dorylus* are currently grouped into six subgenera: *Anomma, Dorylus* and *Rhogmus* are restricted to Africa, whereas *Alaopone* and *Typhlopone* are found also in Asia (Bolton, 1990). The monotypic subgenus *Dichthadia* is endemic to the Oriental Region. The primary study species *D. (Dichthadia) laevigatus* is reported from Burma, Sumatra, Java, Borneo, and Sulawesi (Wilson, 1964). As in all Dorylinae, the brownish yellow workers of *D. laevigatus* are blind and highly polymorphic. In this investigation we distinguish only three morphologically easily recognizable subcastes (minor, media and majors) although intermediate forms exist.

The frequency of *D. laevigatus* was monitored systematically from January until April in six different plots (A-F, Fig. 1) in the vicinity of the Gombak Field Studies Centre (GFSC) of the University of Malaya (Selangor, 3°19′N; 101°45′E; 250 m a.s.l.). The area is mostly covered with advanced secondary forest of the lowland dipterocarp type. The topography is rough, mostly steep hillsides and narrow valley bottoms (Wiedemann, 1969). In addition single sample points were established around the research centre and along the roadside of the nearby Old Bentong Road (Fig. 1).

The plots were distinguished by differences in the mixture of soil components, soil temperature and vegetation. Sand, clay and stony particles were estimated by feel and classified with the standard keys to soil taxonomy (Soil Survey Staff, 1998). Soil temperature was measured using a digital thermometer with the probe placed approximately 3 cm below the soil surface.

Furthermore, the distribution of another hypogaeic Asian species, *D. (Alaopone)* cf. *vishnui,* was documented in India (Goa) and Sri Lanka (Kandy). Finally, the epigaeic foraging African species *D. (Anomma) nigricans* was monitored briefly with the oil-method in the Ivory Coast (Park National de la Comoé).

We first tried to detect *D. laevigatus* in the plots by digging a number of 15–30 cm deep holes into the soil, but did not find a single specimen of this ant by this approach. We then set up a network of sampling points with each point 2.50 m from the next.

Five of the six plots were established at or near the field station about 120–300 m away from each other over an area of approximately 3.5 hectare. The sixth plot (F) was established 3 km to the south of the Field Studies Centre (Fig. 1).

Plot A was enlarged step by step from 49 to 110 sampling points (= 860 m^2, Fig. 2), because in this plot *D. laevigatus* was found early at the borders of the original network. To determine the area

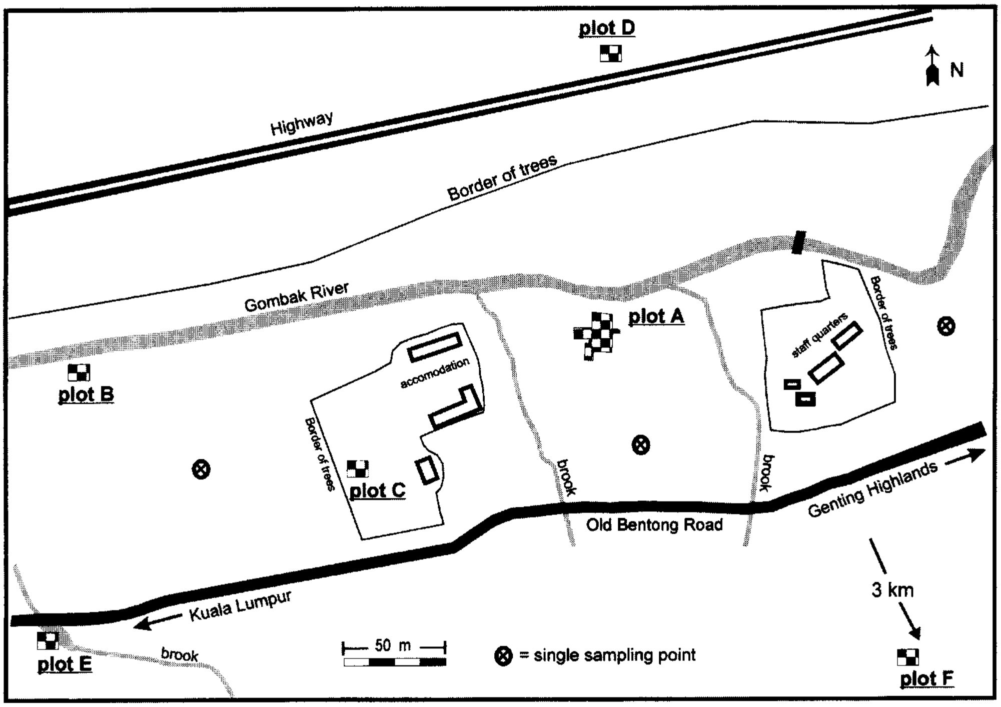

Figure 1. Experimental plots (A–F) and individual baiting stations on the study site at the Ulu Gombak Field Studies Centre (West-Malaysia)

occupied by a single colony, we expanded the plot at the sites with the highest frequency of *D. laevigatus* detection. In plot B (49 sampling points = 225 m^2), C (49), D (5 = 9 m^2) E (49) and F (9 = 25 m^2) the numbers of sampling points remained constant over the investigation period.

Every new sampling point was initially sprinkled with 80 ml of palm oil and in plot A additionally with 40 ml when the plot was enlarged (after the 5th, 12th, 19th, 25th, and 55th day), to prevent a decrease in attractiveness of older sampling points. At the beginning of the investigation we monitored the ant numbers at the sampling points every day by digging a hole 30 cm deep at each of them. Afterwards the oily earth was carefully put back into the hole. After the 11th day we recorded the appearance of workers at intervals of 2–7 days. At each sampling point workers of *D. laevigatus* were extracted from the soil manually, counted and classified by quantity in three groups (a: 1–5 workers, b: 6–29 workers, c: 30 and more workers). As a result, areas of high and low worker frequency could be discriminated. Additionally we placed pieces of toast soaked with oil on the ground surface and covered these baits partly with red glass plates. In this way we were able to observe the ants by day and at night without disturbing them. When these baits became depleted, they were replaced.

We also recorded other ants at the sampling points and recorded their interactions with the *D. laevigatus* workers. An investigation of *D. laevigatus* prey spectra was carried out by burying different subterranean insects, annelids, as well as fresh potatoes in the neighbourhood of highly frequented sampling points. The prey-animals were collected in the soil within the plots and were put into a gauze bag with a mesh wide enough to admit access of minor and media workers of *D. laevigatus* but too small to permit the escape of the prey.

Observations of the hunting and digging behavior of *D. laevigatus* were made on workers from different colonies kept in an earth-filled plastic formicarium (21 cm × 21 cm × 1 cm).

Voucher specimens of ants collected in this study have been deposited at the Staatliches Museum für Naturkunde, Karlsruhe (Germany), the Forschungsinstitut Senckenberg, Frankfurt am Main (Germany) and in the collection of the senior author.

Results

Frequency and geographical distribution of D. laevigatus

Table 1 gives habitat soil horizons, microclimatic conditions, competing ant species and the time between the initial offer of palm oil and the first occurrence of *D. laevigatus* for the six plots. Despite the differences in soil characteristics and temperature *D. laevigatus* appeared in five out of six plots within five days at the latest. Only in plot E no *Dorylus* could

Table 1. Habitat soil horizons, soil temperature at 3 cm, competing ant species and the time between the initial offering of palm oil and the first occurrence of *D. laevigatus* at six plots (A–F) at the Ulu Gombak Field Studies Centre (West-Malaysia)

Plot (no. of baits)	A (110)	B (49)	C (49)	D (5)	E (49)	F (9)
Habitat	secondary forest, dense undergrowth, 3–4 cm leaf litter	forest edge at a river side, only yound trees, 2 cm leaf litter	open grassland, no trees	surrounding vegetation was cut and burnt because of construction of a highway, almost no vegetation	forest edge on a roadside, wet soil, partly flooded	along an old logging road, only yound trees
Soil temperature[a]	25.4 °C	28.6 °C	33 °C	36.7 °C	not measured	27.9 °C
Soil horizon I	0–10 cm	0–8 cm	0–5 cm	no horizons distinguishable	no horizons distinguishable	0–5 cm
	mineral soil, fine sandy loam, many medium sized roots, colour grey, brown	coarse sandy loam with low pebble content, stony, colour grey, brown	coarse sandy loam with gravelly material, colour grey, brown	clay loam, medium sand with 15% coarse sand	wet and muddy soil	clay loam, medium sand, light red brown, ferruginous
Soil horizon II	10–50 cm	8–15 cm get through deeper impossible	5–60 cm	no horizons distinguishable	no horizons distinguishable	5–60 cm
	clay loam, light brown ochre	coarse sandy loam with gravelly material, after 15 cm stones, light brown	gravel and stones			
No. of days until *D. laevigatus* occurred on baits (occupied sample points)	2 (19)	1 (19)	3 (3)	2 (2)	–	2 (3)
Other ants at the baits	*Myrmicaria* sp., *Odontoponera transversa*, *Pheidologeton silenus*, *Cerapachys* spp.	none	*Crematogaster* cf. *artifex*, *Myrmicaria* sp., *Pheidologeton silenus*	none	none	*Myrmicaria* sp.

[a] Measured between 13 hrs and 14 hrs using a digital thermometer with the probe placed approximately 3 cm below the soil surface, air temperature in the shade was 36 °C.

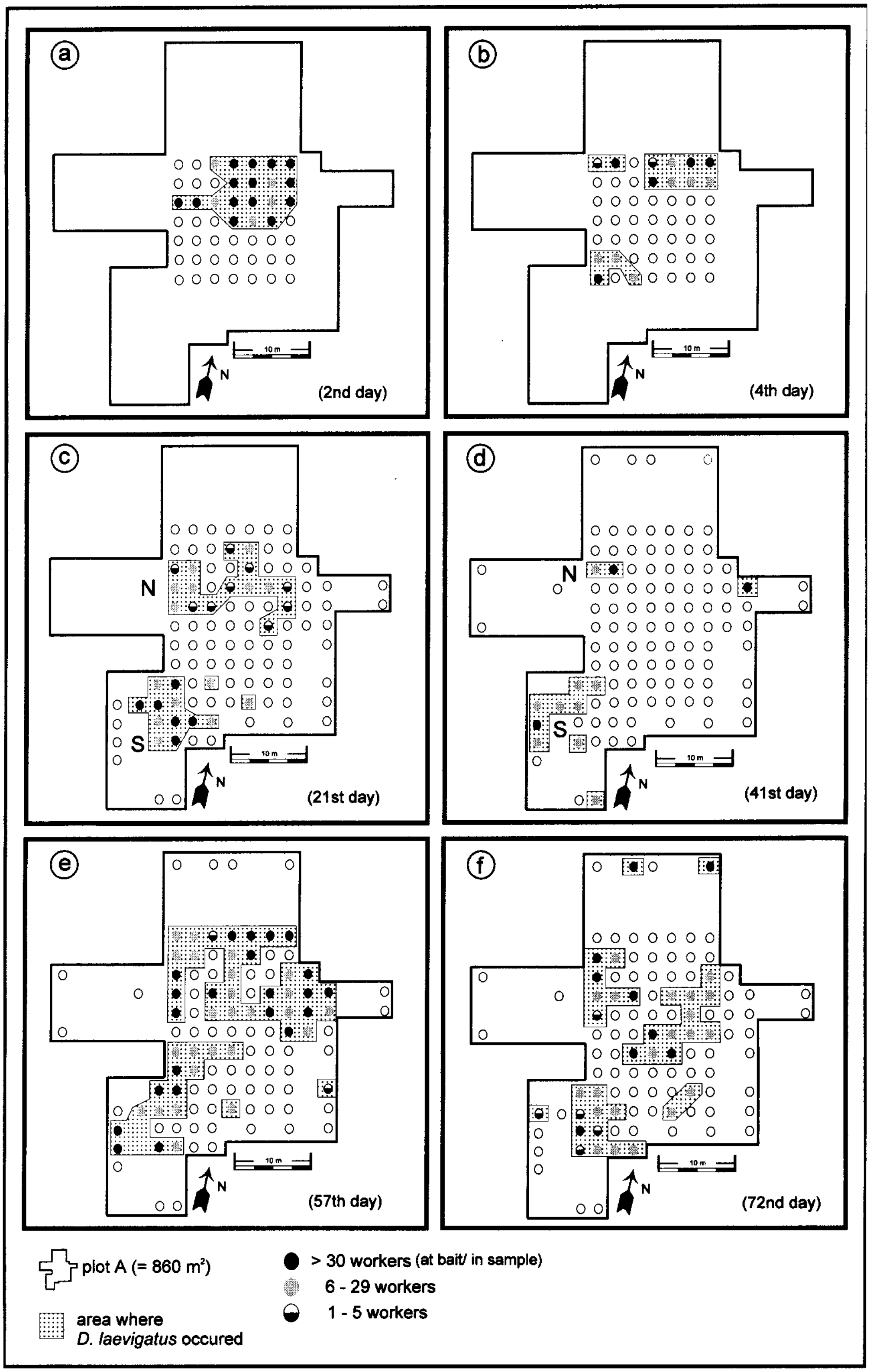

Figure 2 (a–f). Appearance of *D. laevigatus* workers at the baits on different days of the long-term palm-oil-baiting experiment in plot A. Note that during the whole investigation period (72 days) a no-*Dorylus*-land (minimum 5 m) exist between the northern area (N) and the southern area (S) of the plot. This may indicate the border between different colonies. Distance between sampling points was 2.50 m be detected, probably due to the muddy soil. In plot A the loose soil material allowed rapid seeping of the oil, enticing the ants very quickly to come close to the ground surface. Already on the second day 19 sampling points were occupied. In plot B and C soil horizon 2 consisted of gravel and stones, therefore deeper digging was impossible for us. The ants nevertheless found the oil, which had seeped into the soil to a depth of about 15 cm. Even at plot D near the highway, where the soil had been broken up due to building activities one year ago and vegetation had been cut down, which resulted in a very high soil temperature, the ants were found after only two days at the oil baits.

The appearance of *D. laevigatus* at the sampling points was a highly dynamic process, as shown in Figure 2. As early as 48 hours after offering the oil baits, about 73 m^2 out of 860 m^2 of plot A were visited by the army ants (Fig. 2a). At 14 sampling points we found more than 30 workers of all castes. On the fourth day a second area separated by unoccupied oil baits was also visited by *D. laevigatus* (Fig. 2b).

During the 21st and 41st day a shifting of occupied sampling points from the northern area to the southern part was observed (Figs. 2c and 2d). Whereas the southern area (S) was occupied for the whole investigation period (72 days), in the northern part (N) after 41 days almost no ants could be detected (Fig. 2d). After another 40 ml of fresh palm oil was offered on all sampling points on the 55th day, this area again was found to be occupied (Fig. 2e). Whether these two aggregations belong to one colony or represent two different colonies is not known since single isolated individuals put together showed no aggressive behavior even if they come from certainly different colonies (i.e. collected from localities several kilometres apart). At plot A we found the ants for 72 days (Fig. 2f).

In plots B–F palm oil was poured out only once. After four days 19 sampling points (39%) in plot B were occupied by *D. laevigatus*. The highest frequency of workers occurred at the eighth day (24 sampling points). We found *D. laevigatus* for a total of 44 days in plot B. In plots D, E and F as well as on the three single sampling points (Fig. 1), *D. laevigatus* was detected from the beginning until the end of the investigation period (72 days).

When disturbed on the baits during the controls, the ants run away quickly and tried to crawl into the soil. We excavated the soil between several sampling points and found in some cases columns of workers at depths of only 3–10 cm. These subterranean trails were about 1–2 cm broad. Twice we burrowed 1,5 m deep into hard earth and found a network of 3–5 mm small tunnels utilized by *D. laevigatus*.

By using the palm oil baits, distribution of *D. laevigatus* was additionally documented at Genting Highlands (Peninsular Malaysia, Selangor, 3°22′N; 101°45′E; 800-1000 m a.s.l) and in Belum (Peninsular Malaysia, Perak, 5°31′N; 101°25′E; 300 m a.s.l.). Also in Borneo (Poring Hot Springs, 6°03′N; 116°42′E; 500–650 m a.s.l.) and in Sumatra (cultivated area on Lake Maninjau, Barat, 0°20′S; 100°14′E; 600 m a.s.l.) *D. laevigatus* has been found.

In tests with palm oil in Sri Lanka (Kandy, forested and wet area, 7°15′N; 80°37′E;) and in India (Goa, 15°00′N; 74°00′E;) the rare *D. (Alaopone)* cf. *vishnui* was attracted by the baits. In pilot tests at the Ivory Coast (Park National de la Comoé, 9°10′N; 4°20′W; 250 a.s.l.) we found the epigaeic *D. (Anomma) nigricans* frequently on offered oil baits.

Other ants at the baits

Other ants at the baits are listed in Table 1. The first ant to appear at oil baits on the surface was the myrmicine *Myrmicaria* sp. This species nests in the soil and forages both above the ground and in the lower vegetation where it tends homopterans. Also *Crematogaster* cf. *artifex* was attracted, an aggressive territorial ant which nests in arboreal carton nests but forages on the ground as well. We occasionally found single foraging workers of two species of *Cerapachys* (Cerapachyinae) in the soil, but only if no *Dorylus* were present. Whether these ant-hunting species are attracted by the oil is questionable. The ponerine *Odontoponera transversa* was observed selectively preying on *Dorylus* individuals on the ground surface, mostly for minor and media workers.

Behavioral observations

One-hundred-eighty *D. laevigatus* workers of all three size classes (60 individuals each) were placed in a translucent plastic formicarium where their subterranean activities could easily be observed. Workers of all sizes were involved in excavating tunnels. Soil particles were taken with the mandibles and carried away or pushed backwards beneath the body and passed on to the next worker by backward movement of the legs. The minor workers showed the main burrowing activity. However, media and major workers were also involved in grasping and transporting soil particles. The major workers displayed a special digging behavior. By closing the mandibles and moving the head forward up and down they functioned as a kind of "live-hammer". In that way they could successfully loosen soil particles even in hard soil.

On three sampling points (in plot A and plot C) where we offered pieces of toast soaked with oil, *Dorylus* workers were found on the ground surface in large numbers (> 10 000 workers on each bait). The *Dorylus* approached the toast baits by tunnelling through the ground and coming directly from below, after several hours many openings could be found around the baits. Major workers of *D. laevigatus* guarded the oil baits by sitting in the openings in an aggressive posture with permanently widened mandibles and movements of the antennae. Trails on the ground surface connecting different openings (distances 10–50 cm, width = 1,5–3 cm) were guarded by workers of all sizes forming walls with their bodies. Gradually the trails became covered with piled up soil particles eventually forming an incomplete arcade of earthen pellets. On the toast baits we found *D. laevigatus* foraging for 24 hours with no significant activity differences ($\chi^2 = 0,44 < 5,991$). An above-ground confrontation between *Pheidologeton silenus* and *D. laevigatus* on one of these baits

Table 2. Utilization of offered food by the hypogaeic army ant *D. laevigatus*

Food offered	No. of items	No. of items left in cage after 1 day	No of *D. laevigatus* workers found inside cage
Earthworms (Lumbricidae)	8	1 earthworm	10
Earwigs (Dermaptera)	5	cuticle remains	5
Termites (*Macrotermes*)	16	head of termite soldiers	2
Camponotus sp. (Formicidae)	20	head of major workers, cuticle	12
Beetle larvae (Cerambycidae)	3	none	3
Millipedes (Diplopoda)	3	cuticle remains	3
Pieces of raw potatoes	3	3 pieces, nothing taken	2

lasted three weeks (09.03.–29.03.) with frequent alternations of bait ownership. Fights happened in which many members of both colonies were killed. The dead workers remained at the ground surface and were not carried away by *Pheidologeton* or *Dorylus*. When the *Pheidologeton* were in the majority, the *Dorylus* workers closed the entrances and completely disappeared from the ground surface for a maximum of one day. But a little later they again were able, after fighting, to monopolize the food resource for 1–3 days.

Feeding preferences

In food preference tests we offered soldier and worker termites of the genus *Macrotermes* (Macrotermitinae), workers and brood of a soil-nesting *Camponotus* (Formicinae) species, earwigs (Dermaptera), larvae of long-horned beetles (Cerambycidae), millipedes (Diplopoda), earthworms (Lumbricidae) and, as an example of starch-containing vegetables, fresh potatoes.

With the exception of potatoes, the *Dorylus* workers fed on all offered food (Table 2). Workers of *D. laevigatus* (mostly minors and medias) have been found during the controls inside the gauze bags. Within one day most of the prey insects had been torn to pieces and were taken away. In the formicarium a live earthworm lying on the ground was attacked simultaneously and pulled down into the soil by about 20 workers while other workers covered the prey with soil particles.

Discussion

Abundance and distribution

Despite intensive fieldwork of our team during the last 20 years at the Ulu Gombak Field Studies Centre (GFSC) we found *D. laevigatus* accidentally only twice during this time. It turned out that *D. laevigatus* is extremely abundant in this area and was easily discovered also at other sites in Peninsular Malaysia as well as in Borneo and in Sumatra. With the oil monitoring method we are now able to investigate these hypogaeic ants in their whole area of distribution. Furthermore, our first experiences with this simple method in India, Sri Lanka and Africa show that also other species of this genus are attracted by oil. The exclusively hypogaeic *D. (Alaopone) cf. vishnui* had so far only once been reported from Burma (Wheeler, 1913; Wilson, 1964) and had not even been known to occur in India and Sri Lanka. About 60 species of the Old World genus *Dorylus* have been described (Bolton, 1990). Recently, in addition to the four known *Dorylus* species from Asia, two undescribed subterranean species have been found (Dorow et al. in prep., F. Ito pers. comm.) and almost certainly some representatives of this genus remain undiscovered. As mentioned earlier, our knowledge on the biology of this genus is based only on studies of three species of the subgenus *Anomma* raiding and emigrating on the surface of the ground (Raignier and van Boven, 1955; Leroux, 1982; Hölldobler and Wilson, 1990; Bolton, 1995; Gotwald, 1995). However, because these species represent the most advanced Doryline army ants, probably many details of their behavior patterns are atypical and perhaps do not occur in hypogaeic members of the genus. For strictly hypogaeic organism morphological, physiological and behavioral constraints are very different, thus generalizations concerning the sociobiology and ecology of hypogaeic and epigaeic species should be made with great caution.

Palm oil as attractant

Savage (1847) was the first who drew attention to the feeding of palm oil by epigaeic foraging members of the genus *Dorylus*. Gotwald (1974) reported that *D. (Anomma) nigricans* harvest the pithy outer covering of fallen palm nuts and Rettenmeyer et al. (1983) reported that epigaeic *Labidus* spp. in the Neotropics feed on nuts with high contents of oil. No studies about the attractiveness of palm oil to hypogaeic *Dorylus* species have been conducted until now. Astonishingly the palm oil with its enormous energy content attracted only a few other ant species (Table 1). No *Leptogenys* species, not even those with army ant habits, were attracted. Also the column raiding *Aenictus* spp. were never found on the baits, although we observed them foraging in the plots during our investigation. This may be due to their feeding preferences. All *Aenictus* are known to be specialized on ant prey. Particularly *Dorylus* and, to a minor extent, the marauder ant *Pheidologeton silenus*, which is reported also to feed on seeds (Moffett, 1988), seem to be able to metabolize this high energy food resource.

Colony size and behavior

Remarkable is the enormous number of individuals (> 10000) found on single oil baits. Since the proventriculus is degenerate in army ants (Eisner, 1957; Gotwald, 1971), this could be related to the absence of trophallaxis (Gotwald, 1995). Hence the liquid oil probably cannot be passed on from worker to worker or to the larvae. This may be the reason why so many workers appear to feed on the oil. Furthermore, by accumulating huge numbers of individuals at feeding sites of high value, the resource could be monopolized even against powerful competitors like *Pheidologeton silenus*.

Though not investigated in detail, the large number of individuals at baits suggests that *D. laevigatus* may have huge colonies as large as those reported for epigaeic African species (Raignier and van Boven, 1955). The immense mass of individual workers do not only construct chambers for nesting and rearing the brood but also create extensive systems of tunnels and subterranean trails to move through the soil to locate food and for shifting bivouac sites. The clearing and maintenance of these tunnels is a continuous energy consuming process and, as might be expected, they are not transient structures but can persist for many months. The major workers are well adapted to this job since they have big head capsules with strong mandibular muscles which enable them to use their mandibles to break off soil particles and ram paths in the soil. In *D. laevigatus* colonies this worker caste acts not only as defenders but plays an important role in the construction of the trail system. In contrast, particularly the minors may be able to move freely within small pre-existing tunnels (e.g. along root systems) to locate food resources.

Astonishingly in our experiments most of the offered oil baits and even single sampling points outside the plots were detected by the ants. This suggests that they intensively burrow through the soil during the search for food. *D. laevigatus* digs not only in the upper layers of soil but also in the deeper mineral soil layers thus forming a dense three dimensional tunnel system. Because of the reported high frequency of *D. laevigatus* and their abundance below ground one can suspect that these ants must have an enormous influence on the soil fauna. Whether they move randomly through the soil or locate prey by odor or acoustical cues remains an unsolved question.

Although we do not know if the workers on the oil baits in the plots always belonged to only one colony, the fact that we found *D. laevigatus* in plot D, E and F for 3 months even if oil was poured out only once supports the assumption that *D. laevigatus* has a nonphasic, if any emigration pattern. It is therefore conceivable that normally lives in stable, long-term territories like moles. If trophallaxis actually does not occur in *D. laevigatus* and the palm oil is consumed only by the workers, one may assume that the colonies in our plots were not overfed and the long stay on the same site was not correlated with the offering of oil. This means that other food sources, in particular proteins (e.g. soil-inhabiting arthropods and annelids) needed for development of the larvae, would have to be available in adequate amounts to sustain these huge colonies in a limited area.

Food resources

Hypogaeic army ants are generally thought to be prey specialists feeding mainly on social insects (Gotwald, 1995). Schneirla (1971) supposed that hypogaeic army ants are generally termitophagous while epigaeic species are generalists. Rettenmeyer et al. (1983) mentioned that all above ground foraging species of the neotropical genus *Eciton*, the ecological analogues of *Dorylus*, do not kill termites because of the defensive secretions of their nasute soldiers. Our feeding experiments with *D. laevigatus* indicate that this ant is a trophic generalist which feeds on various insects including Macrotermitinae and soil annelids. Whether earth worms and soil nesting termites are dominant natural food resources cannot yet be said. Additional evidence that *D. laevigatus* is not specialized on social insects as prey is given by both the huge colony size as well as the long lasting stay in one area. Particularly the brood of ant colonies and termites represent a temporary rich food resource, but they are widely dispersed and once exploited by army ants it will take some time until the area is colonized again. If *D. laevigatus* depends on social insects it should emigrate frequently and change the trophophoric field.

We have also found *D. laevigatus* feeding on palm fruits in Malaysian oil palm plantations. This indicates that oil rich seeds may form a natural portion of their nutrition. Starch containing vegetables, i.e. potatoes, however, were not collected. Correspondingly *D. laevigatus* is not known to be an agricultural pest. Only one *Dorylus* species, *D.* (*Alaopone*) *orientalis*, is known to feed on various agricultural products which contain no oil but starch and proteins like potatoes, sugar cane, cauliflower, etc. This species is found in China, Nepal, Burma, India, and Sri Lanka (Wilson, 1964) and ranks as a serious agriculture pest (Roonwal, 1975).

Location of nest sites

D. laevigatus usually confines its activities to the underground without external indication of its presence. However, a closer look at the oil plantations of West-Malaysia revealed that the soil between fruits harvested by the army ants was occasionally excavated to the ground surface. In some cases these areas extended to 1–2 m^2, this probably indicated the presence of the nest site. A similar surface sign of the nest is also reported for the African *D. (Anomma) wilverthi* (Raignier and van Boven, 1955).

By using the "oil method" in future investigations and paying attention to above ground soil modifications it should be possible both to find nests of *D. laevigatus* (and maybe other *Dorylus* species) and to find out more about the colony structure. Furthermore, it has to be added that especially army ant nests are valuable resources for symbionts and are often home to hundreds of individual guests of different taxa particularly because of large quantities of stored food (Weissflog et al., 1995, Witte et al., 1999). It is expected that in upcoming studies with the "oil method" many of these ant guests associated with *Dorylus* spp. also will be discovered and could be studied in detail.

Although many questions remain to be answered, the new method seems to be a very promising tool for further research and will yield a better understanding of hypogaeic army ants ecology.

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